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Environmental filtering and taxonomic relatedness underlie the species richness-evenness relationship

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Abstract

We examined the relationship between species richness (S) and evenness (J) within a novel, community assembly framework. We hypothesized that environmental stress leads to filtering (increasing the proportional abundance of tolerant species) and taxonomic dispersion (decreasing the taxonomic relatedness among species within genera and families). Environmental filtering would cause a decline in S by eliminating stress-sensitive species and a reduction of J by allowing only tolerant species to maintain large populations. Taxonomic relatedness would influence both S and J by controlling the nature of interspecific interactions—positive under taxonomic dispersion vs. negative under taxonomic clustering. Therefore, the S-J relationship is a product of environmental filtering and taxonomic relatedness. We tested this framework using continental data on watershed environment and diatom and fish communities in US streams. We confirmed that i) environmental stress, defined by basin forest cover, temperature, and slope, caused filtering (increased tolerant species abundance) and taxonomic dispersion (elevated genus:species and family:species ratios); ii) both S and J declined with filtering but increased with taxonomic clustering; and iii) the role of filtering on J was pronounced only under stressful conditions, while taxonomic clustering remained an important predictor of J across stressful and benign environments.

Key words: community assembly; competition; complementarity; functional groups; limiting similarity; stress gradient hypothesis

Introduction

Two aspects of biodiversity, namely richness (S) or the number of species in a community and evenness or the equitability in species' abundance (J), have drawn considerable interest in ecology because of their correlations with important community properties, such as biomass production and decomposition, susceptibility to invaders, stress resistance, and extinction risks (Wilsey & Potvin, 2000; Kennedy et al., 2002; Dangles & Malmqvist, 2004; Wittebolle et al., 2009; Blois et al., 2010). The relationship of S and J has also been extensively investigated across habitats and organismal groups, including algae, plants, fungi, invertebrates, and vertebrates, and shown to depend on both the environment and the level of species richness, i.e. the shape of the relationship changes at a threshold richness (Stirling & Wilsey, 2001; Bock et al., 2007; Soininen et al., 2012). This implies that both abiotic and biotic forces affect the S-J relationship but their relative importance is not well understood. Here, we explore the relationship between S and Pielou's evenness (J) from the perspective of community assembly theory to address a fundamental ecological question—what is the interplay between environmental stress and biotic forcing in driving the patterns of biodiversity?

Two seemingly opposing theories have been invoked to explain community assembly at local scales—limiting similarity and environmental filtering (Weiher & Keddy, 1995; Mayfield & Levine, 2010; HilleRisLambers et al., 2012). According to the limiting similarity model (MacArthur & Levins, 1967), competition for limiting resources selects for niche differentiation and trait divergence among coexisting species. In contrast, the environmental filtering idea proposes that the environment supports only species with converging traits that confer positive fitness under the local conditions (Keddy, 1992). Both limiting similarity (Stubbs & Wilson, 2004; Montaña et al., 2014) and environmental filtering (Peres-Neto 2004; Mouillot et al., 2007;

67 Mouchet et al., 2013) have been shown to shape local communities. Here we suggest that these
68 processes may function together in controlling the patterns of biodiversity (Fig. 1).
69 Environmental filtering under stressful conditions will reduce richness by allowing
70 growth of only a small subset of the regional pool that exhibits survival traits, e.g. tolerance to
71 resource limitation or disturbance, although some poorly adapted species can also be present due
72 to random dispersal. Filtering will also decrease evenness because it disrupts the balance
73 between growth and immigration of the resident species—tolerant species can reproduce and
74 grow in numbers, while the populations of the less tolerant species will be supported exclusively
75 by immigration and will remain small (Passy, 2016). Consistent with these expectations, both
76 richness and evenness have been reported to decline with environmental stress (Sabater, 2000;
77 Feio et al., 2010; Murphy & Romanuk, 2014; Passy, 2016). However, to share the limited niche
78 space in unfavorable environments, tolerant species must diverge in coexistence traits, ensuring
79 complementary resource acquisition, e.g. microhabitat or diet preferences.
80 In benign conditions, the environmental filtering weakens and more species from the
81 regional pool, including sensitive forms, can reproduce, contribute significantly to community
82 biomass, and increase both richness and evenness. Favorable habitats have longer and more
83 numerous environmental gradients, i.e. more diverse gradient structure, due to the emergence of
84 complex environment-community interactions. For example, in running waters, the thick benthic
85 mats developing in productive habitats generate longer internal resource gradients than the thin
86 biofilms in unproductive streams (Stevenson & Glover, 1993; Passy, 2008). It has been
87 suggested that a diverse gradient structure is linked to greater niche overlap and phylogenetic
88 similarity among coexisting species, while simplified gradient makeup, to stronger niche
89 differentiation and increased phylogenetic distinction (Passy & Legendre, 2006). The argument

90 is that variability in resource supply allows coexistence of species with small differences in
91 resource requirements, expressed as divergence at a species level. In contrast, when the gradient
92 structure is simplified and gradients are short or non-existent, species must either utilize different
93 resources or develop different disturbance adaptations to avoid competitive exclusion. Such large
94 physiological and/or morphological differences are associated with greater taxonomic
95 divergence, e.g. at the genus and family categories (Passy & Legendre, 2006). Thus, we expect
96 stressful conditions to restrict biota to a few tolerant (filtering) but taxonomically dissimilar
97 species (limiting similarity), whereas benign conditions to provide for a greater diversity of
98 taxonomically related forms (Fig. 1a).

99 As phylogenetic structure determines the distribution of traits, it is linked to species
100 interactions, e.g. competition and complementarity (Webb et al., 2002; HilleRisLambers et al.,
101 2012), which may impact the relationship between richness and evenness. Evenness can increase
102 at low richness as a result of positive interactions (complementarity or facilitation) among
103 taxonomically distant species (Fig. 1). For example, under stressful nitrogen limiting conditions,
104 nitrogen fixers stimulate biomass production of distantly related non-nitrogen fixers through
105 facilitation (Agawin et al., 2007). Conversely, negative interactions (competition among
106 taxonomically similar species) can elevate evenness at high richness by preventing dominance
107 (Fig. 1). This model can explain the shift in species interactions from negative (competition) to
108 positive (complementarity and facilitation) with the transition of the environment from benign to
109 harsh (Bertness & Callaway, 1994; Bruno et al., 2003; Wang et al., 2013) as a consequence of
110 trait convergence corresponding to increased taxonomic clustering.

111 Here, we used continental data on watershed characteristics, and diatom and fish
112 communities in US streams to test our predictions (Fig. 1). The degree of environmental filtering

was measured by the ratio (ST) of species sensitive vs. tolerant of environmental stress, e.g. resource limitation and physical or chemical disturbance. Thus, low ST ratios (higher abundance of tolerant species), found in harsh environments, indicated filtering (selection for survival traits), while high ST ratios (numerical dominance of sensitive species) were suggestive of environmental favorability. Evaluating the form of species interactions (positive vs. negative) is intractable but it is expected to correlate with phylogenetic distance with low values (phylogenetic similarity) linked to competition (Violle et al., 2011) and high values (phylogenetic dissimilarity), to facilitation and complementarity (Valiente-Banuet & Verdu, 2007; Venail & Vives, 2013). Nevertheless, the relationship between phylogenetic distance and interspecific interactions has been controversial (Venail et al., 2014) and further research is necessary to confirm whether the hypothesized correlations do exist in the organismal groups studied here. We adopted the ratio of higher taxa richness to species richness, which reflects the taxonomic redundancy within terminal groups, as a proxy measure of species interactions. Low ratios (taxonomic similarity) were likely to be associated with competition, whereas high ratios (taxonomic dissimilarity), with complementarity.

To assess the effects of environmental filtering and taxonomic clustering on S, J, and their relationship, we constructed a structural equation model (SEM) (Fig. 1b). We used the family:species (FS) ratio to represent taxonomic clustering (low FS values indicating high taxonomic clustering), but the same results are expected with the genus:species ratio. The sensitive:tolerant (ST) species ratio reflected environmental filtering (low ST values indicating strong filtering). Given their opposing behavior along the environmental favorability gradient (Fig. 1a), the FS ratio and the ST ratio were projected to be negatively correlated (Fig. 1b). The

SEM also predicted similar responses of S and J to the FS and ST ratios, and consequently, a positive S-J relationship.

Materials and methods

We used stream community data from most major watersheds and aquifers in the US, generated by the NAWQA program of the US Geological Survey (see http://water.usgs.gov/nawqa/). There were 2822 algal samples from 1435 distinct stream localities, spanning 40 latitudinal and 87 longitudinal degrees. Quantitative samples were collected by the USGS between 1993 and 2009 from the richest-targeted habitats (RTH), comprising riffles or woody snags. A total of 1698 taxa, primarily identified to species, belonged to 117 genera and 46 families. For all constituent taxa, we had data on population density (cells·cm^{-2}) and were able to classify 1692 of them into low profile (189 taxa), high profile (604 taxa), and motile guilds (899 taxa), according to Passy (2007) and Rimet & Bouchez (2012). Low profile species are of short habit and tolerant of resource limitation and physical disturbance, while high profile species, having tall stature, and motile species are sensitive to these stressors (Passy, 2007). The 189 tolerant species came from 16 genera and 9 families, while the 1503 sensitive species, from 102 genera and 44 families, resulting in genus to species ratios of 0.08 in the tolerant group and 0.07 in the sensitive group and family to species ratios of 0.05 and 0.03 in the respective groups. A ratio of sensitive to tolerant species (ST), calculated as ln (high profile + motile cell density +1)/(low profile cell density +1), was used as a measure of filtering. Dominance of tolerant species (ln ST ratio < 0) was considered indicative of environmental stress, while dominance of sensitive species (ln ST ratio ≥ 0), of favorable environmental conditions.

There were 2194 qualitative fish samples with a total abundance between 5 and 9331 individuals. Preliminary research showed that in samples with ≥455 counted individuals, species richness was very weakly dependent on abundance and, therefore, reliably measured (Passy, 2016). Consequently, we used only the 761 fish samples with ≥455 counted individuals where we observed a total of 460 species from 117 genera and 42 families. These samples were collected between 1993 and 2010 from 399 distinct localities. For the most abundant 216 species, comprising 83% of the total sample abundance, classification into tolerant, moderate, and intolerant of environmental stress was possible, based on data from the Environmental Protection Agency (http://water.epa.gov/scitech/monitoring/rsl/bioassessment/app_c-2.cfm) and NAWQA (http://water.usgs.gov/nawqa/ecology/data.html). The 18 tolerant species belonged to 15 genera and 7 families, the 134 moderate species, to 62 genera and 24 families, and the 64 intolerant species, to 26 genera and 11 families. The genus to species ratios were 0.83 in the tolerant group and 0.41 in the intolerant group, while the family to species ratios were 0.39 and 0.17 in the respective groups. An ST ratio was calculated as ln (intolerant individuals + 1)/(tolerant individuals + 1) and used as a metric of filtering. As in diatoms, communities with ln ST ratio < 0 were viewed as developing under environmental stress and those with ln ST ratio ≥ 0, under environmental favorability.

In diatoms and fish, the number of all species (i.e., richness), Pielou's evenness (J), and the ratios of genus to species (GS) and family to species richness (FS) were recorded for each sample. A decrease in GS or FS indicates taxonomic clustering, i.e. species tend to come from the same genera or families. Data on basin climate, topography, hydro-modification, and land use, available for 2575 diatom and 732 fish samples, comprised the environmental dataset.

Redundancy analyses with forward selection and 999 Monte Carlo permutations (CANOCO 4.5, 1997-2009 Biometris – Plant Research International, Wageningen, The Netherlands) were performed on diatom and fish correlation matrices to test whether the environment had significant effects on filtering and taxonomic relatedness, as hypothesized in Fig. 1. The environmental dataset consisted of 43 appropriately transformed (ln- or arcsine square root transformed) watershed variables. The dependent dataset included the ST ratio and the ratios of genus to species- (GS) and family to species (FS) richness. The environmental variables with the strongest and significant effects on the dependent set were retained in the final RDA model.

All bivariate relationships, including J, S, ST-, GS-, and FS ratios, were modelled with linear or non-linear equations, selected for their good fit, parsimony, and high R^2 after running a curve-fitting procedure (TableCurve 2D 5.01, SYSTAT Software, Inc., Chicago IL, USA, 2002). The variance in J explained by the predictors individually and interactively, was determined by multiple regressions, followed by variance partitioning using SYSTAT 13.1 (SYSTAT Software, Inc. 2009). Structural equation modelling was performed with SYSTAT 13.1 to test the predictions in Fig. 1b. Goodness of fit was measured by a discrepancy function or root mean square error of approximation (RMSEA).

Results

The variables with the strongest impact on the ratios of sensitive to tolerant species (ST), genus to species (GS), and family to species richness (FS) were the following in the order of their selection by the RDA with percent explained variance given in parentheses (p = 0.001 for all variables): forest cover (9.3%), drainage area (4.6%), and slope (2.6%) in diatoms; and

deciduous forest cover (14.6%), air temperature (11.7%), and agriculture (12.4%) in fish (Fig. 2a, b). The total explained variance was moderate (39% in fish) to low (17% in diatoms). The first RDA axis in both analyses captured most to nearly all of the explained variance and represented a stress gradient. Small forested streams in watersheds of high slopes provided a stressful environment for diatoms, while cold streams with low deciduous forest cover were stressful to fish, evident in the negative correlation of these factors with the ST ratios. As hypothesized in Fig. 1, the increase in the ST ratio was paralleled by a decrease in the GS and FS ratios.

In both diatoms and fish evenness increased with richness but in diatoms, the S-J relationship was comparatively strong (R^2 = 0.50, Fig. 3a), while in fish, it was much weaker (R^2 = 0.08, Fig. 4a). In both groups, evenness was also constrained by the ST ratio (Figs 3b, 4b) and FS ratio (Figs 3c, 4c). Evenness increased sharply as the dominance of tolerant species decreased, but changed little in low stress communities where sensitive/intolerant forms prevailed, evident in the steepness of the regression slope in these two groups (Figs 3b, 4b). A quadratic function of the ST ratio captured well the saturation of J under sensitive species dominance. In contrast, the relationships of evenness with both richness and FS ratio were comparatively strong in both low stress and high stress communities (Figs 3, 4). This means that while the environmental effect on J was weak in favorable conditions (shallow J-ln ST slope at ln ST ratio ≥ 0), the species interaction effect remained strong across harsh and benign environments. From the two metrics of taxonomic similarity, the genus to species ratio was a weaker predictor of J—after the family to species ratio entered the model, the GS ratio added only 2% to the explained variance in diatoms and 0% in fish. Consequently, we used only the FS ratio in all regression analyses of J and S.

In both groups richness increased sharply with the ST ratio under stressful conditions, but in benign environments, there was a difference between the two groups. Diatom richness changed little, while fish richness continued to increase (Fig. 5). Additional *t*-tests revealed significantly higher values for S and significantly lower values for FS ratio in low (ln ST ratio ≥ 0) than in high stress (ln ST ratio < 0) communities ($p < 0.001$, diatoms and fish). These results indicated that species-poor communities in stressed environments comprised taxonomically distant species, while species-rich communities in benign environments, taxonomically related species.

Structural equation models (SEMs) demonstrated that in diatoms and fish the ST ratio and the FS ratio were negatively correlated, as predicted in Fig. 1 (Fig. 6). Both S and J were constrained by the ST ratio, representative of environmental filtering. The linear and quadratic terms of the ST ratio, signifying saturating responses of S and J, were significant in both models except for fish richness, which increased linearly with the ST ratio. The FS ratio was a negative predictor of both S and J, which were the highest when the communities were most taxonomically clustered (lowest FS ratios). The S-J relationship was positive in diatoms, but due to collinearity of S with the FS ratio, it became negative in fish. All other relationships in both SEMs were consistent with the respective bivariate relationships (Figs 3-5). The SEM models further demonstrated that both the FS and the ST ratios had significant direct effects on J. The two SEMs had overall excellent fits—the discrepancy function in the diatom model (0 degrees of freedom, DF) was $7.98e^{-11}$ and the RMSEA in the fish model (1 DF) was <0.001.

Discussion

Environmental stress, represented by greater forest cover and basin slope in diatoms but lower deciduous forest cover and temperature in fish, generated two gradients of community response—a shift in species tolerance concurrent with a change in taxonomic clustering, as predicted in Fig. 1. Small, forested streams in high elevation watersheds were stressful to algae due to light and nutrient deficiency (Hill et al., 2011). Streams with reduced forest cover were stressful to fish because their lower substrate stability and heterogeneity provide fewer spawning habitats and limited macroinvertebrate prey (Allan, 2004). Lower temperatures were also stressful to fish, evident in the increased abundance of tolerant species. Across both organismal groups, filtering in unfavorable environments resulted in dominance of a small number of tolerant but comparatively taxonomically diverse species. Conversely, numerical abundance of a large number of sensitive but comparatively taxonomically similar forms was characteristic for benign habitats. In fact, taxonomic dispersion of tolerant species and taxonomic clustering of sensitive species were detected not only locally but also in the regional pools. Thus regionally, the genus to species ratios were 1.2 to 2.1 times higher and the family to species ratios, 1.6 to 2.3 times higher in the tolerant than in the sensitive group across diatoms and fish. This suggests that the patterns of local taxonomic similarity emerge as a consequence of environmental selection for functional groups, which differ not only in stress tolerance but also in taxonomic distances. Therefore, taxonomic clustering and overdispersion in local communities are environmentally imposed and may control the form of interspecific interactions. These findings are in agreement with experimental data showing that nutrient stress in stream biofilms causes a reduction in species richness at the expense of sensitive forms but an increase in taxonomic distance among the surviving tolerant species (Larson & Passy, 2013). Although we did not assess traits other than tolerance, our results on taxonomic distances, likely to correlate with trait differences in

general, provide evidence that environmental filtering and limiting similarity may not be opposing processes, as generally considered (Weiher & Keddy, 1995; Mouillot et al., 2007; Mouchet et al., 2013; Montaña et al., 2014), but inherently linked from the local to the regional scale, as suggested in Fig. 1.

Consistent with our expectations, environmental stress caused filtering of species with convergent survival traits but potentially disparate coexistence traits. As discussed, the prevailing diatoms and fish in stressful conditions were tolerant (low ST ratios). Tolerance is associated with distinct body sizes in both diatoms and fish (Passy, 2012), which in turn determine various aspects of species' physiology and life history with an influence on survival, including growth and metabolic rates, time of reproductive maturity, life span, and pollution tolerance (Peters, 1983; Cattaneo et al., 1998; Brown et al., 2002). However, the most common tolerant diatoms, *Cocconeis placentula et* vars and *Achnanthidium minutissimum*, tend to exhibit microhabitat preference for macrophytes and hard substrates, respectively (Passy et al., 1999; Soininen & Eloranta, 2004). The three most abundant tolerant fish differed in diet and microhabitat, e.g. *Rhinichthys atratulus* is an invertivore, inhabiting rocky substrates and gravel; *Semotilus atromaculatus* is an invertivore and carnivore, with a preference for rocky substrates and sand; and *Pimephales promelas* is a detritivore and invertivore, found in sandy and muddy habitats (http://water.usgs.gov/nawqa/ecology/data.html). Therefore, tolerant species across diatoms and fish may diverge in coexistence traits but a more detailed trait analysis is needed to fully support this hypothesis. Previous research showed that environmental filtering and limiting similarity may not be mutually exclusive mechanisms of community assembly if they constrain complementary sets of traits, e.g. those associated with large- vs. small scale components of the niche, respectively (Ackerly & Cornwell, 2007; Ingram & Shurin, 2009). Specifically,

environmental filtering defines the beta niche, or the species' position along broad environmental gradients, while limiting similarity constrains the alpha niche, or traits linked to local habitat utilization (Ackerly & Cornwell, 2007). To what extent tolerance and coexistence traits describe the alpha and beta niche is unclear; nevertheless, it is conceivable that these traits may be under distinct selection pressure and experience differential convergence and divergence along environmental gradients.

Our study further showed that environmental filtering and taxonomic clustering, which varied predictably along the environmental stress gradient (Figs 1a, 2), underlay the relationship of richness and evenness as both S and J responded to these factors in a similar fashion (Fig. 6). In both diatoms and fish, the S-J relationship was positive across stressful and benign conditions. Environmental filtering, i.e. the increase in tolerant species abundance, caused a sharp decline in both richness and evenness. When sensitive species began to dominate and increase in proportion under benign conditions, evenness and diatom richness displayed little change, while fish richness alone showed a positive response. This differential behavior of fish S and J can contribute to their weaker relationship compared to diatoms. In contrast, taxonomic clustering correlated strongly with evenness across stressful and favorable conditions. Communities with the highest richness and evenness, found in benign environments, displayed the lowest FS ratios. These results suggest that environmental filtering has a more restricted influence on community evenness, i.e. only under stress, whereas taxonomic clustering is an important predictor across environmental conditions. Although we do not know to what degree traits are conserved across phylogenetically similar species, we can speculate that in environmentally stressed and impoverished communities the addition of taxonomically distant species that may acquire resources in a complementary fashion increases J. Other positive interspecific interactions, such

316 as direct facilitation and habitat amelioration, which are important in high stress environments
317 (Bertness & Callaway, 1994; He et al., 2013), can also contribute to the positive S-J relationship.
318 Conversely, diverse communities, developing under benign conditions, have more species per
319 genus and family, which are more likely to compete for the shared resources. Competition
320 among ecologically and competitively similar species can lead to coexistence of a large number
321 of species (Scheffer & van Nes, 2006), and as we see here, high richness is also associated with
322 high abundance equitability. Given the within family taxonomic homogenization occurring with
323 the increase in richness, the S-J relationship may be driven by environmental filtering and
324 positive interactions at low S but negative interactions at high S. However, the SEMs also
325 revealed that taxonomic clustering and environmental filtering had independent effects on J that
326 were not related to richness, adding to earlier findings that richness and evenness have
327 complementary responses to the environment (Hillebrand et al. 2007).

328 Prior research on fish, implying either environmental (Oberdorff et al., 1998) or biotic
329 control (Montaña et al., 2014) in structuring these communities, has been controversial. This
330 investigation demonstrates that both factors are influential but while environmental filtering
331 weakens under favorable conditions, the role of taxonomic clustering in determining evenness
332 remains unaltered. Although we have not measured directly species interactions, our framework
333 may be used to resolve the contradiction between the stress gradient hypothesis, stating that the
334 prominence of positive interactions increases with environmental stress (Bertness & Callaway,
335 1994; He et al., 2013), and the dogma in animal ecology that competition intensifies in harsh,
336 unproductive environments (Barrio et al., 2013). In exploring continental gradients of
337 environmental and biotic variability, we showed that stressful environments were inhabited by a
338 significantly more species-poor but less taxonomically clustered fauna (higher FS ratios).

Therefore, harsh conditions are less conducive to competition but more prone to positive interspecific interactions than benign habitats but confirmation of these ideas requires experimental research on species interactions along environmental gradients. Thus, merging the view of community assembly through environmental filtering and competitive interactions (Weiher & Keddy, 1995) with the stress gradient hypothesis (Bertness & Callaway, 1994) may provide a more complete understanding of the mechanisms of species coexistence.

References

Ackerly, D. D.& W. K. Cornwell, 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. Ecology Letters 10: 135-145.

Agawin, N. S. R., S. Rabouille, M. J. W. Veldhuis, L. Servatius, S. Hol, H. M. J. van Overzee & J. Huisman, 2007. Competition and facilitation between unicellular nitrogen-fixing cyanobacteria and non-nitrogen-fixing phytoplankton species. Limnology and Oceanography 52: 2233-2248.

Allan, J. D., 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. Annual Review of Ecology Evolution and Systematics 35: 257-284.

Barrio, I. C., D. S. Hik, C. G. Bueno & J. F. Cahill, 2013. Extending the stress-gradient hypothesis - is competition among animals less common in harsh environments? Oikos 122: 516-523.

Bertness, M. D.& R. Callaway, 1994. Positive interactions in communities. Trends in Ecology & Evolution 9: 191-193.

Blois, J. L., J. L. McGuire & E. A. Hadly, 2010. Small mammal diversity loss in response to late-Pleistocene climatic change. Nature 465: 771-774.

Bock, C. E., Z. F. Jones & J. H. Bock, 2007. Relationships between species richness, evenness, and abundance in a southwestern savanna. Ecology 88: 1322-1327.

363 Brown, J. H., V. K. Gupta, B. L. Li, B. T. Milne, C. Restrepo & G. B. West, 2002. The fractal nature of
364 nature: power laws, ecological complexity and biodiversity. Philosophical Transactions of the
365 Royal Society of London Series B-Biological Sciences 357: 619-626.
366 Bruno, J. F., J. J. Stachowicz & M. D. Bertness, 2003. Inclusion of facilitation into ecological theory.
367 Trends in Ecology & Evolution 18: 119-125.
368 Cattaneo, A., A. Asioli, P. Comoli & M. Manca, 1998. Organisms' response in a chronically polluted lake
369 supports hypothesized link between stress and size. Limnology & Oceanography 43: 1938-1943.
370 Dangles, O.& B. Malmqvist, 2004. Species richness-decomposition relationships depend on species
371 dominance. Ecology Letters 7: 395-402.
372 Feio, M. J., C. N. Coimbra, M. A. S. Graca, S. J. Nichols & R. H. Norris, 2010. The influence of extreme
373 climatic events and human disturbance on macroinvertebrate community patterns of a
374 Mediterranean stream over 15 y. Journal of the North American Benthological Society 29: 1397-
375 1409.
376 He, Q., M. D. Bertness & A. H. Altieri, 2013. Global shifts towards positive species interactions with
377 increasing environmental stress. Ecology Letters 16: 695-706.
378 Hill, W. R., B. J. Roberts, S. N. Francoeur & S. E. Fanta, 2011. Resource synergy in stream periphyton
379 communities. Journal of Ecology 99: 454-463.
380 Hillebrand, H., D. S. Gruner, E. T. Borer, M. E. S. Bracken, E. E. Cleland, J. J. Elser, W. S. Harpole, J. T.
381 Ngai, E. W. Seabloom, J. B. Shurin & J. E. Smith, 2007. Consumer versus resource control of
382 producer diversity depends on ecosystem type and producer community structure, Proceedings of
383 the National Academy of Sciences (USA) 104: 10904-10909.
384 HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine & M. M. Mayfield, 2012. Rethinking
385 Community Assembly through the Lens of Coexistence Theory. Annual Review of Ecology
386 Evolution and Systematics 43: 227-248.

387 Ingram, T.& J. B. Shurin, 2009. Trait-based assembly and phylogenetic structure in northeast Pacific
388 rockfish assemblages. Ecology 90: 2444-2453.
389 Keddy, P. A., 1992. Assembly and response rules: two goals for predictive community ecology. Journal
390 of Vegetation Science 3: 157-164.
391 Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman & P. Reich, 2002. Biodiversity as a
392 barrier to ecological invasion. Nature 417: 636-638.
393 Larson, C. A.& S. I. Passy, 2013. Rates of species accumulation and taxonomic diversification during
394 phototrophic biofilm development are controlled by both nutrient supply and current velocity. Appl.
395 Environ. Microbiol. 79: 2054-2060.
396 MacArthur, R.& R. Levins, 1967. The limiting similarity, convergence, and divergence of coexisting
397 species. American Naturalist 101: 377-385.
398 Mayfield, M. M.& J. M. Levine, 2010. Opposing effects of competitive exclusion on the phylogenetic
399 structure of communities. Ecology Letters 13: 1085-1093.
400 Montaña, C. G., K. O. Winemiller & A. Sutton, 2014. Intercontinental comparison of fish
401 ecomorphology: null model tests of community assembly at the patch scale in rivers. Ecological
402 Monographs 84: 91-107.
403 Mouchet, M. A., M. D. M. Burns, A. M. Garcia, J. P. Vieira & D. Mouillot, 2013. Invariant scaling
404 relationship between functional dissimilarity and co-occurrence in fish assemblages of the Patos
405 Lagoon estuary (Brazil): environmental filtering consistently overshadows competitive exclusion.
406 Oikos 122: 247-257.
407 Mouillot, D., O. Dumay & J. A. Tomasini, 2007. Limiting similarity, niche filtering and functional
408 diversity in coastal lagoon fish communities. Estuarine Coastal and Shelf Science 71: 443-456.
409 Murphy, G. E. P.& T. N. Romanuk, 2014. A meta-analysis of declines in local species richness from
410 human disturbances. Ecology and Evolution 4: 91-103.

411 Oberdorff, T., B. Hugueny, A. Compin & D. Belkessam, 1998. Non-interactive fish communities in the
412 coastal streams of North-western France. Journal of Animal Ecology 67: 472-484.
413 Passy, S. I., 2007. Diatom ecological guilds display distinct and predictable behavior along nutrient and
414 disturbance gradients in running waters. Aquatic Botany 86: 171-178.
415 Passy, S. I., 2008. Continental diatom biodiversity in stream benthos declines as more nutrients become
416 limiting. Proceedings of the National Academy of Sciences (USA) 105: 9663-9667.
417 Passy, S. I., 2012. A hierarchical theory of macroecology. Ecology Letters 15: 923-934.
418 Passy, S. I., 2016. Abundance inequality in freshwater communities has an ecological origin. American
419 Naturalist 187: 502-516.
420 Passy, S. I.& P. Legendre, 2006. Power law relationships among hierarchical taxonomic categories in
421 algae reveal a new paradox of the plankton. Global Ecology and Biogeography 15: 528-535.
422 Passy, S. I., Y. Pan & R. L. Lowe, 1999. Ecology of the major periphytic diatom communities from the
423 Mesta River, Bulgaria. International Review of Hydrobiology 84: 129-174.
424 Peres-Neto, P. R. 2004. Patterns in the co-occurrence of fish species in streams: the role of site suitability,
425 morphology and phylogeny versus species interactions. Oecologia 140:352-360.
426 Peters, R. H., 1983. The ecological implications of body size. Cambridge University Press, Cambridge,
427 UK.
428 Rimet, F. & A. Bouchez, 2012. Life-forms, cell-size and ecological guilds of freshwater diatoms.
429 Knowledge and Management of Aquatic Ecosystems 406: 01, DOI: 10.1051/kmae/2012018.
430 Sabater, S., 2000. Diatom communities as indicators of environmental stress in the Guadiamar River, S-
431 W. Spain, following a major mine tailings spill. Journal of Applied Phycology 12: 113-124.
432 Scheffer, M.& E. H. van Nes, 2006. Self-organized similarity, the evolutionary emergence of groups of
433 similar species. Proceedings of the National Academy of Sciences of the United States of America
434 103: 6230-6235.

435 Soininen, J.& P. Eloranta, 2004. Seasonal persistence and stability of diatom communities in rivers: are
436 there habitat specific differences? European Journal of Phycology 39: 153-160.
437 Soininen, J., S. Passy & H. Hillebrand, 2012. The relationship between species richness and evenness: a
438 meta-analysis of studies across aquatic ecosystems. Oecologia 169: 803-809.
439 Stevenson, R. J.& R. Glover, 1993. Effects of algal density and current on ion transport through
440 periphyton communities. Limnology and Oceanography 38: 1276-1281.
441 Stirling, G.& B. Wilsey, 2001. Empirical relationships between species richness, evenness, and
442 proportional diversity. American Naturalist 158: 286-299.
443 Stubbs, W. J. & J. B. Wilson, 2004. Evidence for limiting similarity in a sand dune community. Journal of
444 Ecology 92: 557-567.
445 Valiente-Banuet, A.& M. Verdu, 2007. Facilitation can increase the phylogenetic diversity of plant
446 communities. Ecology Letters 10: 1029-1036.
447 Venail, P. A. & M. J. Vives, 2013. Phylogenetic distance and species richness interactively affect the
448 productivity of bacterial communities. Ecology 94: 2529-2536.
449 Venail, P. A., A. Narwani, K. Fritschie, M. A. Alexandrou, T. H. Oakley & B. J. Cardinale, 2014. The
450 influence of phylogenetic relatedness on species interactions among freshwater green algae in a
451 mesocosm experiment, Journal of Ecology 102: 1288-1299.
452 Violle, C., D. R. Nemergut, Z. C. Pu & L. Jiang, 2011. Phylogenetic limiting similarity and competitive
453 exclusion. Ecology Letters 14: 782-787.
454 Wang, J., C. B. Zhang, T. Chen & W. H. Li, 2013. From selection to complementarity: the shift along the
455 abiotic stress gradient in a controlled biodiversity experiment. Oecologia 171: 227-235.
456 Webb, C. O., D. D. Ackerly, M. A. McPeek & M. J. Donoghue, 2002. Phylogenies and community
457 ecology. Annual Review of Ecology and Systematics 33: 475-505.
458 Weiher, E. & P. A. Keddy, 1995. Assembly rules, null models, and trait dispersion: new questions from
459 old patterns. Oikos 74: 159-164.

460 Wilsey, B. J.& C. Potvin, 2000. Biodiversity and ecosystem functioning: Importance of species evenness
461 in an old field. Ecology 81: 887-892.
462 Wittebolle, L., M. Marzorati, L. Clement, A. Balloi, D. Daffonchio, K. Heylen, P. De Vos, W. Verstraete
463 & N. Boon, 2009. Initial community evenness favours functionality under selective stress. Nature
464 458: 623-626.

Figure legend

Figure 1. (a) Conceptual model identifying the processes underlying the variability in community richness and evenness. Environmental favorability reduces the role of filtering (elimination of sensitive species) but increases the taxonomic clustering of local biota, which has an impact on species interactions. Positive interactions are expected among taxonomically distant species, while negative interactions will predominate among taxonomically similar species. Since richness and evenness exhibit similar behavior along these gradients, their relationship is expected to be positive. Taxonomic clustering is assessed by the family:species (FS) ratio and filtering, the sensitive:tolerant (ST) species ration. **(b)** Structural equation model predicting the causal relationships among the FS ratio, the ST ratio, S and J. e_1 and e_2 = error terms.

Figure 2. Redundancy analyses of the ratios of sensitive to tolerant species, genus to species, and family to species richness showing the most important environmental predictors in diatoms **(a)** and fish **(b)**. The variance explained by each axis is given in percent. n = 2575 samples (a) and 732 samples (b). The environmental variables were measured in percent cover for forest, deciduous forest and agriculture, km^2 for basin drainage area, percent for mean basin slope, and °C for temperature.

Figure 3. Diatoms. Relationships of evenness (J) with richness (S) **(a)**, ratio of sensitive to tolerant species (ST) **(b)**, and ratio of family to species richness (FS) **(c)**. In a-c, the overall fit is given as a solid blue curve, while the fits for stressed communities (ln ST < 0, in red) and non-stressed communities (ln ST ≥ 0, in black) are given as long- vs. short-dashed blue curves,

488 respectively (logarithmic in a and linear in b-c). Note in (a) the steeper increase in J with S under
489 stressful conditions. The regression model and statistics for the overall fits are shown in the
490 panels. n = 2800 samples.
491
492 **Figure 4. Fish.** Relationships of evenness (J) with richness (S) **(a)**, ratio of intolerant to tolerant
493 species (ST) **(b)**, and ratio of family to species richness (FS) **(c)**. In a-c, the overall fit is given as
494 a solid blue line, while the fits for stressed communities (ln ST < 0, in red) and non-stressed
495 communities (ln ST ≥ 0, in black) are given as long- vs. short-dashed blue lines, respectively.
496 Note in (a) the steeper increase in J with S under stressful conditions. The regression model and
497 statistics for the overall fits are shown in the panels. n = 761 samples.
498
499 **Figure 5.** Relationships of ln richness with ratio of sensitive to tolerant species in diatoms (n =
500 2803 samples) **(a)** and fish (n = 761 samples) **(b)**. The overall fit (quadratic in a and linear in b) is
501 given as a solid blue curve, while the fits for stressed communities (ln ST < 0, in red) and non-
502 stressed communities (ln ST ≥ 0, in black) are given as dashed blue lines. The regression model
503 and statistics for the overall fits are shown in the panels.
504
505 **Figure 6.** Structural equation models (SEMs) for diatoms (n = 2800 samples) **(a)** and fish (n =
506 761 samples) **(b)** showing only the significant paths (p < 0.05) with the corresponding
507 standardized coefficients. The relationships are causative (one-headed arrows) or correlative
508 (two-headed arrows). e_1 and e_2 = error terms.
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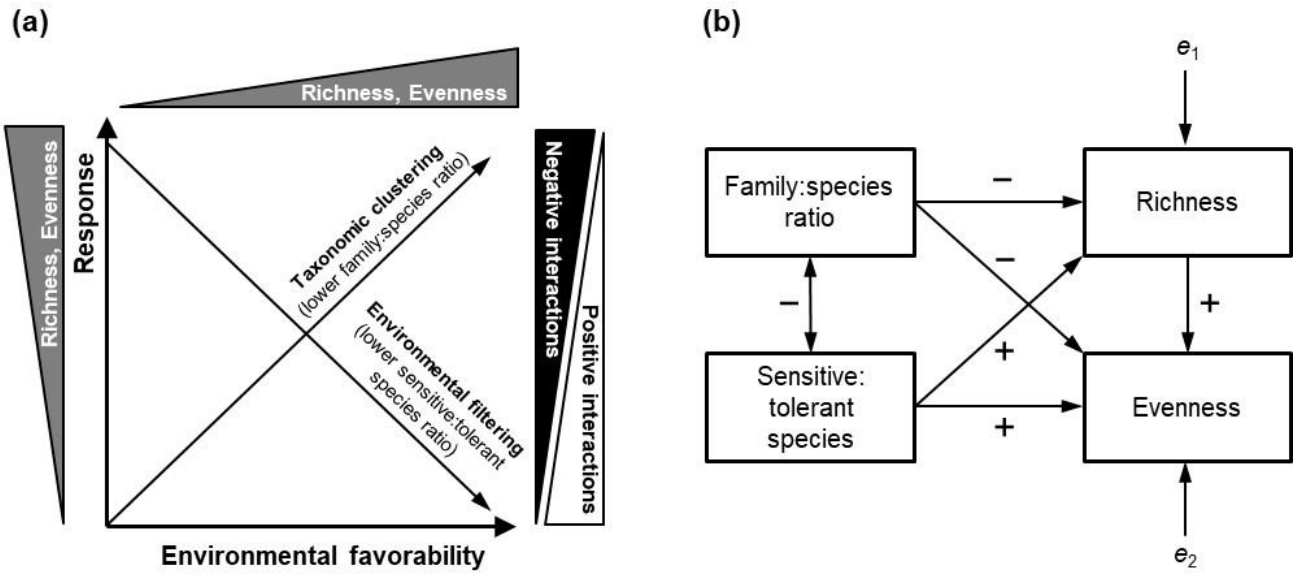

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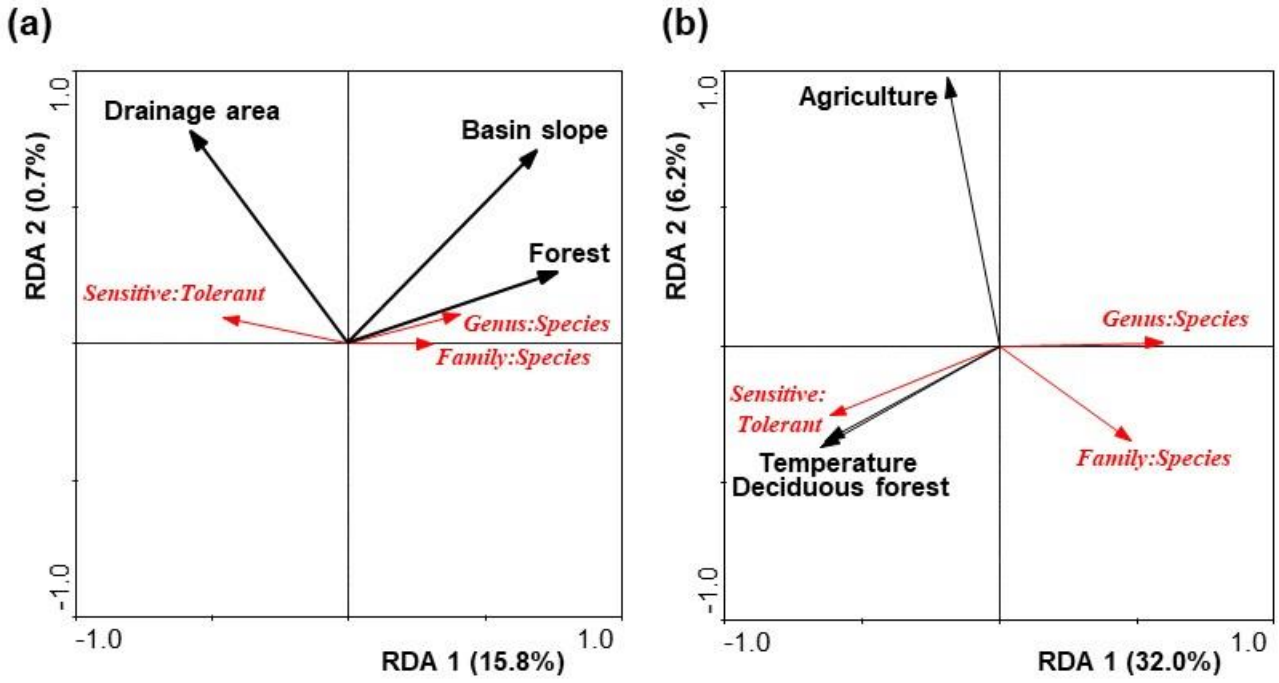
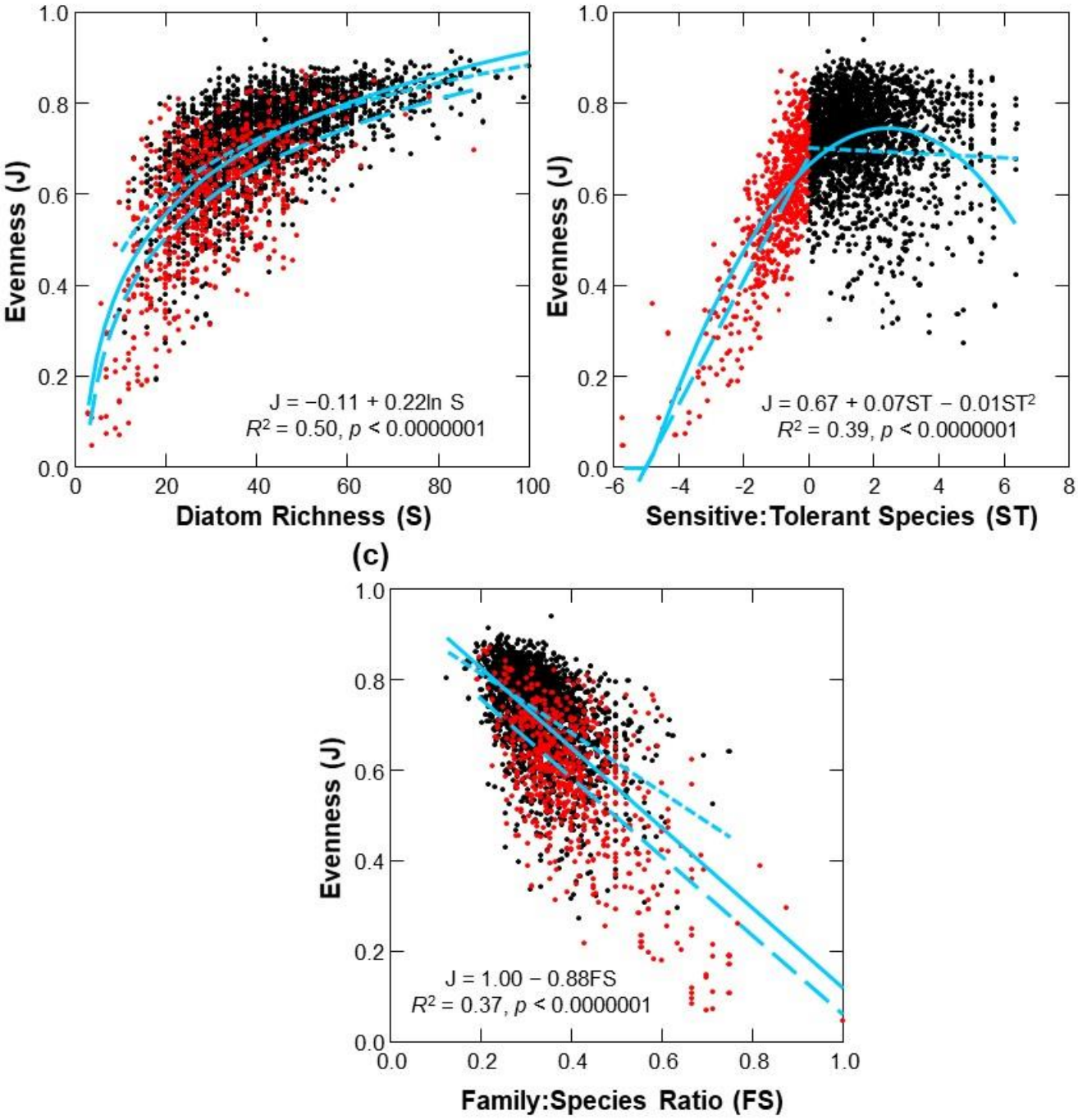
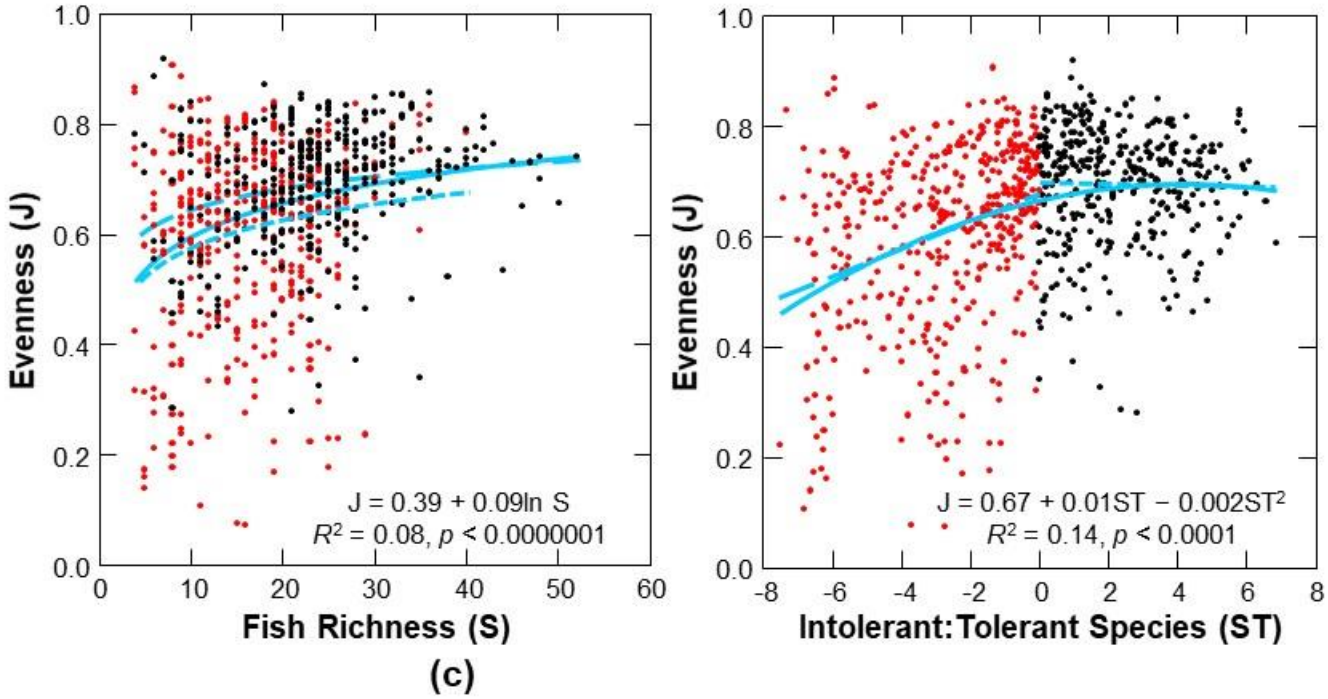
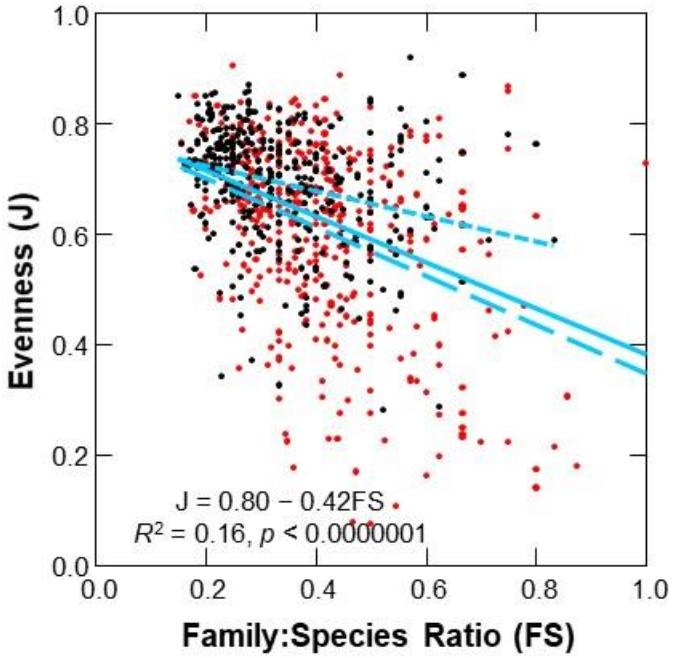

(a)
Drainage area
Basin slope
Forest
Sensitive:Tolerant
Genus:Species
Family:Species
RDA 2 (0.7%)
RDA 1 (15.8%)
1.0
-1.0
(b)
Agriculture
Genus:Species
Sensitive:
Tolerant
Temperature
Deciduous forest
Family:Species
RDA 2 (6.2%)
RDA 1 (32.0%)


Evenness (J)
Diatom Richness (S)
J = −0.11 + 0.22ln S
R² = 0.50, p < 0.0000001
Sensitive:Tolerant Species (ST)
J = 0.67 + 0.07ST − 0.01ST²
R² = 0.39, p < 0.0000001
(c)
Family:Species Ratio (FS)
J = 1.00 − 0.88FS
R² = 0.37, p < 0.0000001



(c)



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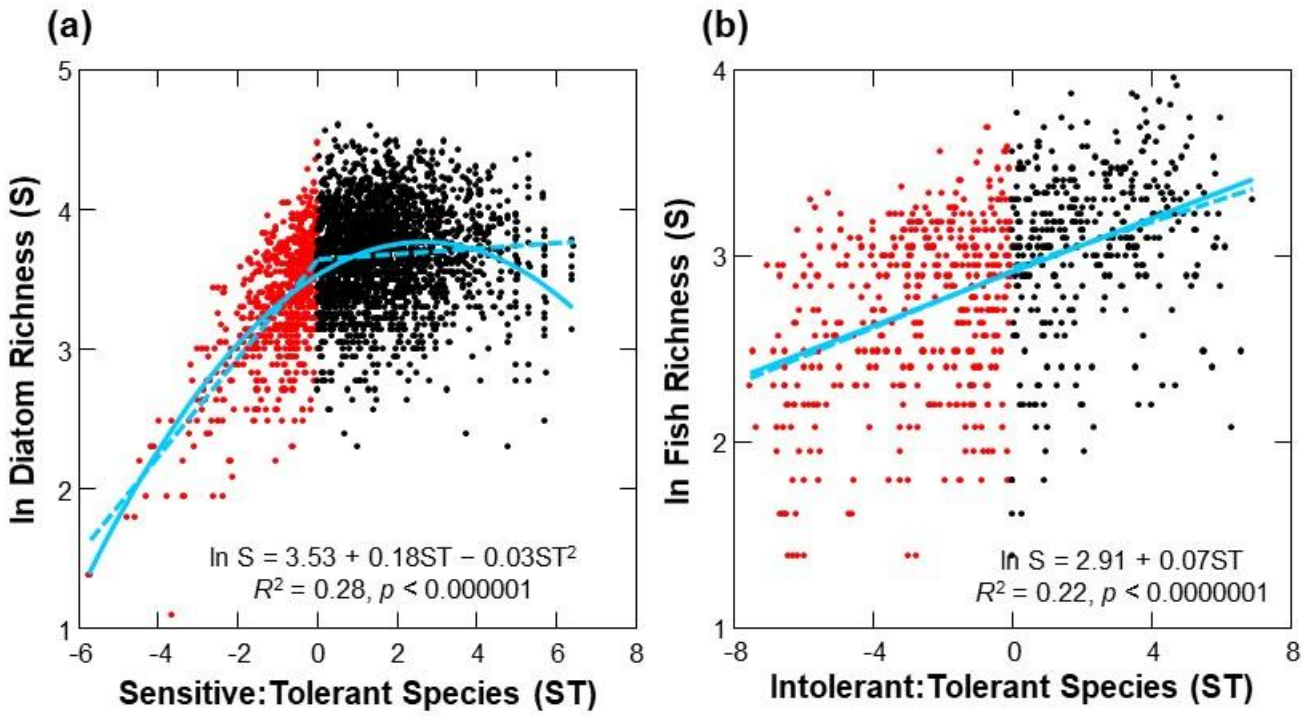
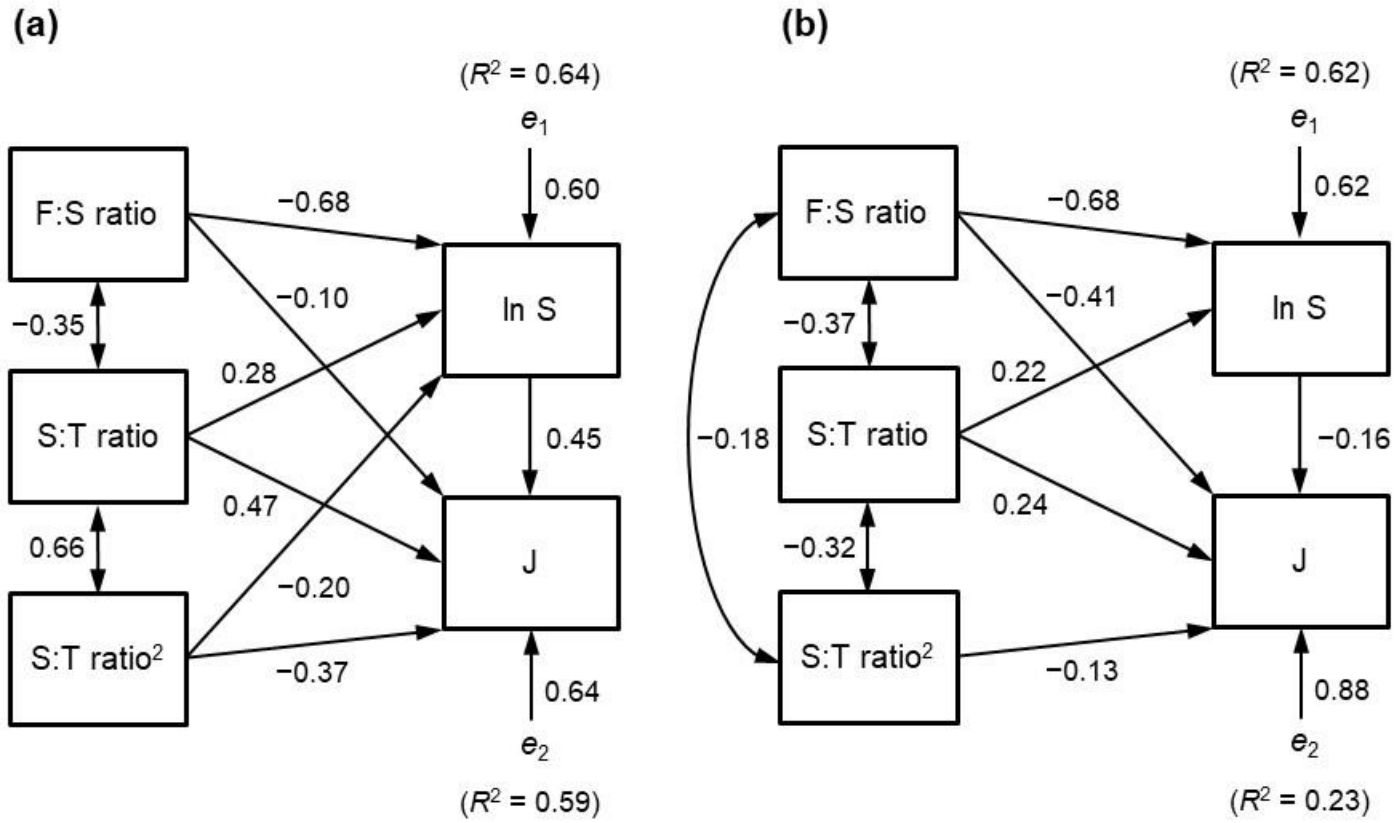

(a)
ln Diatom Richness (S)
Sensitive:Tolerant Species (ST)
ln S = 3.53 + 0.18ST − 0.03ST²
R² = 0.28, p < 0.000001
(b)
ln Fish Richness (S)
Intolerant:Tolerant Species (ST)
ln S = 2.91 + 0.07ST
R² = 0.22, p < 0.0000001



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